

## Inter-Generic Variation in the External Male Genitalia of the Subfamily Microgastrinae (Hymenoptera, Braconidae), with a Reassessment of Mason's Tribal System

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**Abstract.**—External male genitalia of 39 genera of Microgastrinae, 2 of Cardiochilinae and one of Miracinae were examined to reappraise Mason's tribal system of the braconid subfamily Microgastrinae. Volsellar structures of the male genitalia came to provide useful new characters. On the basis of morphological characters including those of the male genitalia, monophyly of Mason's tribes and their groups was reassessed. The tribes Apanellini and Microgastrini (except for *Sathon*) most likely form a monophyletic group, although monophyly of each tribe is not supported by the evidence. The placement of *Prasmodon* and *Sathon* in the Microgastrini is doubtful, and the latter may belong to the monophyletic assemblage composed of the Cotesiini, Microplitini and Forniciini. The Cotesiini is probably paraphyletic since some of the members seem to be close to the Microplitini and Forniciini.

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### INTRODUCTION

With about 1300 described species worldwide, the Microgastrinae is the second largest braconid subfamily in terms of number of species (Shaw and Huddleston, 1991), and it is one of the most important components of the parasitoid complex of many lepidopteran pests in forestry and agriculture (e.g., Gauld and Bolton 1988, Austin and Dangerfield 1992). Members of the subfamily are koinobiont endoparasitoids of lepidopteran larvae and are associated with symbiotic polydnnaviruses (Shaw and Huddleston 1991, Stoltz and Whitfield 1992, Sharkey 1993, Wharton 1993).

The monophyly of the Microgastrinae is firmly established by the unique flagellum with invariably 16 articles, most of which typically have 2 ranks of longitudinal plaques (Mason 1981). Also, Mason (1981, 1983) suggested some additional autapomorphies to define this subfamily. It is widely accepted that the Microgastrinae forms a monophyletic group with the Car-

diochilinae, Khoikhoiinae and Miracinae, though the relationships among them have not been firmly resolved (Mason 1983, Quicke and van Achterberg 1990, Wharton et al. 1992, Whitfield and Mason 1994).

Current framework of the generic and tribal systematics of the Microgastrinae was proposed by Mason (1981), who split the large genus *Apanteles* (*sensu* Nixon 1965) into 23 genera and recognized 50 extant genera arranged in five tribes, Apanellini, Microgastrini, Forniciini, Cotesiini and Microplitini. His generic concept was quite close to the species groups of *Apanteles* defined by Nixon (1965), which had been largely taken from the idea of Wilkinson (1932).

Mason's generic classification has been adopted by many taxonomists (e.g., Williams 1985, 1988, Marsh et al. 1987, Papp 1988, Austin and Dangerfield 1992), though Tobias (1986) and Shaw and Huddleston (1991) withheld total approval of his generic proposals. Mason's phylogenetic analysis and suprageneric classifica-

tion of the Microgastrinae, however, have been criticized by Walker et al. (1990), who concluded that Mason's tribes are not established on the basis of synapomorphies. Recent authors (Shaw and Huddleston 1992, Austin and Dangerfield 1992) also hesitated to adopt Mason's tribal system of the Microgastrinae. There is a need of further intensive research to understand the phylogenetic framework of this large and economically important subfamily.

Mason's classification is principally based on structures of the female genitalia. As shown by Tobias (1967), Marsh (1965), Quicke (1988) and Quicke and van Achterberg (1990), the male genitalia can provide useful characters for the higher level classification of braconids. Except for Williams' (1988) revisional study of *Sathlon*, however, most systematic studies on the Microgastrinae have given little attention to the male genitalia. The present paper reports on the volsellar structures of the external male genitalia in the Microgastrinae to elucidate their inter-generic variations. I have examined 39 out of 53 extant genera of the Microgastrinae, and also several genera of the Cardiochilinae and Miracinae as outgroups. On the basis of morphological data including those of the male genitalia, I will reappraise Mason's tribal system.

## MATERIALS AND METHODS

The species examined are listed in Table 1. The microgastrines are arranged in Mason's tribal system; *Austrocotesia* is tentatively placed in the Apantelini. As outgroups of the Microgastrinae, *Cardiochiles* and *Hartenita* (Cardiochilinae) and *Mirax* (Miracinae) were examined.

Metasomata of the dried specimens were immersed for 2–3 days in 5% KOH at 40°C. Genitalia were removed from the rest of the metasoma and rinsed with 70% ethanol.

Volsellae were torn away from surrounding cuticle and mounted in glyceri-

ne on slides. They were measured and photographed with a Nikon light microscope.

Terms for male genitalia are taken from Snodgrass (1941). The volsella of the Braconidae consists of lamina volsellaris (l) and two distal lobes, digitus (digitus volsellaris, d) and cuspis (cuspis volsellaris, c) (Figs. 1, 3). At the apex of a median longitudinal ridge (volsellar ridge, r), the lamina volsellaris is distally articulated with the digitus. The cuspis is continuous with the lamina volsellaris in the Microgastrinae and related subfamilies (Quicke and van Achterberg 1990).

Length of the lamina volsellaris was measured from the basal end of the lamina volsellaris to the apical end of the volsellar ridge. Digital length was measured from the apical end of the volsellar ridge to the apex of the digitus.

## RESULTS AND DISCUSSION

### Descriptions of Volsellae

**Microgastrinae: Apantelini.** Lamina volsellaris with 1–8 (usually 2–5) setae or setal alveoli (Table 1). Cuspis glabrous, separated from digitus except for *Miropotes*, in which they were fused with each other and so volsella became a single plate (Figs. 7–8). Relative length of digitus to lamina volsellaris 0.39 to 0.69 (Table 1). In *Apanteles*, *Austrocotesia*, *Dolichogenidea*, *Papanteles*, *Pholetesor*, *Promicrogaster* and *Sen-daphne*, digitus arched dorsally or crescent-shaped, distinctly convex ventrally, with a pointed apex directed dorsally or laterally (Figs. 1–5, 9, 11–13); in *Illidops*, digitus tubiform apically and strongly arched dorsally (Fig. 6); in *Miropotes*, digitus convex ventrally with the apex rather round (Fig. 7) or crescent-shaped (Fig. 8); in *Pellicope*, digitus only slightly convex ventrally, not crescent-shaped, while the apical portion obviously bent dorsally (Fig. 10). Apex of digitus with 1–4 (usually 2–3) teeth (Table 1).

**Microgastrinae: Microgastrini.** Lamina

Table 1. Lamina volsellaris and digitus of Microgastrinae, Cardiochilinae and Miracinae.

Taxon	Origin and number of specimens	Length of lamina volsellaris (mm)	No. of setae on lamina volsellaris <sup>a</sup>	Digitus/lamina volsellaris length	No. of apical teeth of digitus	Shape of digitus <sup>b</sup>
<b>MICROGASTERINAE</b>						
<b>Apantelini</b>						
<i>Apanteles baldufi</i> Muesebeck	USA (1)	0.16	3	0.58	2	A, C (Fig. 1)
<i>Apanteles conopiae</i> Watanabe	Japan (2)	0.22–0.25	6–8	0.46–0.52	2	A, C
<i>Apanteles crassicornis</i> (Provancher)	Canada (1)	0.3	3–4	0.51	2	A, C
<i>Apanteles cypris</i> Nixon	Japan (5)	0.17–0.20	2–5	0.44–0.51	2	A, C (Fig. 2)
<i>Apanteles murinanæ</i> Capek & Zwoelfer	Switzerland (1)	0.23	3–4	0.48	2	A, C
<i>Apanteles nephoteris</i> (Packard)	Canada (1)	0.22	3	0.41	2	A, C
<i>Apanteles xanthostigma</i> (Haliday)	Europe (1)	0.17	3	0.55	1	A, C
<i>Austrocotesia delicata</i> Austin & Dangerfield	New Guinea (1)	0.11	3	0.45	1–2	A, C (Fig. 3)
<i>Dolichogenidea absona</i> (Muesebeck)	Canada (1)	0.20	3	0.44	2	A, C
<i>Dolichogenidea conspersae</i> (Fiske) comb. nov. = <i>Apanteles conspersae</i> Fiske, 1911	Japan (5)	0.15–0.17	3–4	0.44–0.54	2	A, C
<i>Dolichogenidea dilecta</i> (Haliday)	Slovakia (1)	0.20	4	0.42	2	A, C
<i>Dolichogenidea infima</i> (Haliday)	Hungary (1)	0.18	2–3	0.49	2	A, C (Fig. 4)
<i>Dolichogenidea nixosiris</i> (Papp)	Mongolia (1)	0.16	2	0.54	2	A, C (Fig. 5)
<i>Dolichogenidea</i> sp. ( <i>laevigata</i> species-group)	Japan (5)	0.18–0.21	3–4	0.48–0.55	2	A, C
<i>Illidops</i> sp.	Canada (1)	0.26	7	0.39	2	T, C (Fig. 6)
<i>Miopotes kilkuhnii</i> Austin	Australia (1)	0.15	(1)	0.52	2	O–R, C (Fig. 7)
<i>Miopotes thuraris</i> Austin	New Hebridis (1)	0.17	2	0.46	2	A, C (Fig. 8)
<i>Papanteles peckorum</i> Mason	Ecuador (1)	0.21	3–4	0.69	3	A, C (Fig. 9)
<i>Pelicope yuccamica</i> Mason	USA (1)	0.28	2	0.57	3–4	O, S (Fig. 10)
<i>Pholetesor bicolor</i> (Nees)	Hungary (2)	0.13	2	0.48–0.54	2	A, C
<i>Pholetesor circumscriptus</i> (Nees)	Hungary (1)	0.13	2	0.49	2	A, C
<i>Pholetesor salalicus</i> (Mason)	USA (1)	0.14	2	0.48	1	A, C
<i>Pholetesor viminetorum</i> (Wesmael)	USA (1)	0.17	3	0.46	2	A, C (Fig. 13)
<i>Promicrogaster</i> sp.	Brazil (1)	0.17	3–4	0.55	3	A, C (Fig. 11)
<i>Sendaphne</i> sp.	Ecuador (1)	0.20	5–6	0.60	2	A, C (Fig. 12)
<b>Microgastrini</b>						
<i>Choeras consimilis</i> (Viereck)	Canada (1)	0.19	3	0.42	2	A, C
<i>Choeras psarae</i> (Wilkinson)	Nepal (1)	0.23	2	0.54	2	A, C (Fig. 14)
<i>Choeras takeuchii</i> (Watanabe) comb. nov. = <i>Microgaster takeuchii</i> Watanabe, 1937	Japan (6)	0.23–0.28	2–3	0.46–0.57	2–3	A, C (Fig. 15)
<i>Hygroplitis melligaster</i> (Provancher)	Canada (1)	0.25	4	0.34	2	O, C–S
<i>Hygroplitis russatus</i> (Haliday)	Japan (3)	0.28	2–4	0.46–0.48	3	O, C (Fig. 19)
<i>Hypomicrogaster ecdytolophae</i> (Muesebeck)	Canada (1)	0.18	3	0.48	2–3	A, C (Fig. 16)
<i>Iconella etellae</i> (Viereck)	Mexico (1)	0.26	4–5	0.49	2	A, C (Fig. 17)
<i>Iconella</i> sp.	Japan (2)	0.23	3–4	0.58	2	A, C
<i>Microgaster australis</i> Thomson	Spain (1)	0.23	3	0.46	2–3	A, C (Fig. 18)
<i>Microgaster canadensis</i> Muesebeck	Canada (1)	0.23	2	0.46	2–3	O, C
<i>Microgaster gelechia</i> Riley	Canada (1)	0.30	2	0.45	4	O, C
<i>Microgaster hospes</i> Marshall	Hungary (1)	0.23	2	0.50	3	O, C
<i>Microgaster kudingensis</i> Wilkinson	Japan (2)	0.28	3	0.50–0.52	3	O, C (Fig. 20)
<i>Microgaster subcompleta</i> Nees	Japan (2)	0.26–0.28	2–3	0.45–0.52	2–3	O, C
<i>Microgaster tibialis</i> Nees	Hungary (2)	0.24	2–3	0.45–0.47	3	O, C
<i>Paroplitis</i> cf. <i>wesmaeli</i> (Ruthe)	Japan (1)	0.14	3–4	0.62	2	A, C (Fig. 21)

Table 1. Continued

Taxon	Origin and number of specimens	Length of lamina volsellaris (mm)	No. of setae on lamina volsellaris*	Digitus/lamina volsellaris length	No. of apical teeth of digitus	Shape of digitus†
<i>Prasmodon</i> sp.	Brazil (1)	0.27	2	0.46	4-5	A-R, S (Fig. 22)
<i>Pseudapanteles annulicornis</i> Ashmead	Panama (1)	0.15	2	0.45	2	A, C (Fig. 23)
<i>Rhygoplitis aciculatus</i> Ashmead	St. Lucia (1)	0.17	3	0.51	2	A, C (Fig. 25)
<i>Sathon lateralis</i> (Haliday)	Ireland (1)	0.20	3	0.44	2	R, S (Fig. 24)
<i>Sathon masoni</i> Williams	USA (1)	0.22	7	0.44	2	N, C-S (Fig. 27)
<i>Sathon neomexicanus</i> (Muesebeck)	USA (1)	0.52	7	0.50	2	T, C (Fig. 26)
<i>Xanthomicrogaster</i> sp.	Ecuador (1)	0.21	1	0.46	2	A, C-S (Fig. 28)
<b>Forniciini</b>						
<i>Fornica arata</i> (Enderlein)	Taiwan (1)	0.27	2	0.46	3-4	R, C
<i>Fornica ceylonica</i> Wilkinson	Taiwan (1)	0.21	2	0.53	3	R, C-S (Fig. 29)
<b>Cotesiini</b>						
<i>Buluka achterbergi</i> Austin	Pen. Malaysia (1)	0.13	(3)	0.49	2	R, C (Fig. 34)
<i>Cotesia affinis</i> (Nees)	Japan (5)	0.15-0.17	12-15	0.47-0.51	3-4	R, S
<i>Cotesia ancilla</i> (Nixon)	Japan (1)	0.13	8-10	0.49	3	R, S
<i>Cotesia flavipes</i> Cameron	Japan (3)	0.16-0.19	6-7	0.27-0.35	2	R, S
<i>Cotesia glomerata</i> (L.)	Japan (4)	0.14-0.16	6-9	0.37-0.46	2-3	R, S
<i>Cotesia kariyai</i> (Watanabe)	Japan (2)	0.20	8-10	0.35	3	R, S
<i>Cotesia melanoscelus</i> (Ratzeburg)	Canada (1)	0.13	13	0.45	4	R, S (Fig. 36)
<i>Cotesia ofella</i> (Nixon)	Italy (1)	0.15	10-13	0.40	3	R, S
<i>Cotesia plutellae</i> (Kurdjumov)	Japan (3)	0.12	10-13	0.42-0.47	3	R, S
<i>Cotesia rubecula</i> (Marshall)	Canada (1)	0.15	10-12	0.43	3	R, S
<i>Cotesia tatehae</i> (Watanabe)	Japan (5)	0.17-0.20	7-8	0.38-0.46	4-6	R, S (Fig. 37)
<i>Cotesia tenebrosa</i> (Wesmael)	Iraq (1)	0.13	8-9	0.42	4	R, S
<i>Deuterixys carbonaria</i> (Wesmael)	Sweden (1)	0.10	2	0.47	2	R, S (Fig. 38)
<i>Deuterixys pacifica</i> Whitfield	USA (1)	0.09	2	0.46	2	R, S
<i>Diolcogaster abdominalis</i> (Nees)	Hungary (1)	0.20	6-7	0.46	4	R, S (Fig. 39)
<i>Diolcogaster duris</i> (Nixon)	Mexico (1)	0.18	5-6	0.50	2	R, S
<i>Diolcogaster cf. spreta</i> (Marshall)	Japan (5)	0.13-0.15	3-5	0.49-0.52	3-4	R, C (Fig. 40)
<i>Distatrix papilionis</i> (Viereck)	India (2)	0.16	1	0.40-0.44	2	R, C-S (Fig. 41)
<i>Exix mexicana</i> Mason	Mexico (1)	0.18	6-7	0.49	2-3	R, S (Fig. 42)
<i>Glyptapanteles aliphera</i> (Nixon)	Netherlands (1)	0.17	4-5	0.45	2	R, S (Fig. 46)
<i>Glyptapanteles fulvipes</i> (Haliday)	Japan (5)	0.16-0.18	6-7	0.36-0.41	2	R, S
<i>Glyptapanteles liparidis</i> (Bouche)	Japan (5)	0.20-0.24	9-13	0.44-0.51	4-5	R, S (Fig. 47)
<i>Glyptapanteles websteri</i> (Muesebeck)	Canada (1)	0.11	2	0.49	2	R, S
<i>Lathrapanteles fuscus</i> Williams	Canada (1)	0.20	7-8	0.45	2	N, C-S (Fig. 35)
<i>Protopanteles alaskensis</i> Ashmead	Canada (1)	0.14	7	0.43	2	R, S
<i>Protopanteles anchisiades</i> (Nixon)	Slovakia (1)	0.17	7	0.42	2	R, S
<i>Protopanteles lymantriae</i> (Marsh)	Japan (2)	0.16	6-9	0.37-0.45	2-3	R, S (Fig. 43)
<i>Protomicroplitis calliptera</i> (Say)	USA (1)	0.23	4-6	0.54	2	R, S
<i>Protomicroplitis mediatius</i> (Cresson)	Cuba (1)	0.27	6-7	0.43	2	R, C (Fig. 44)
<i>Rasivalva rugosa</i> (Muesebeck)	USA (1)	0.17	2-3	0.41	2	R, S (Fig. 45)
<i>Rasivalva stigmatica</i> (Muesebeck)	Canada (1)	0.18	4-5	0.47	2	R, S
<i>Venanides xeste</i> Mason	Canada (1)	0.15	1-2	0.37	3	R, C-S (Fig. 48)
<i>Venanus pinicola</i> Mason	USA (1)	0.09	(1)	0.46	2	R, S (Fig. 49)
<i>Wilkinsonellus striatus</i> Austin & Dangerfield	New Guinea (1)	0.15	(2)	0.52	2	R, C-S (Fig. 50)
<b>Microplitini</b>						
<i>Alloplitis completus</i> Nixon	Pen. Malaysia (1)	0.17	2	0.47	2	R, S (Fig. 33)
<i>Microplitis atamiensis</i> Ashmead	Japan (4)	0.17-0.22	2-4	0.42-0.49	2-3	R, S (Fig. 30)
<i>Microplitis deprimator</i> (Fabricius)	Japan (3)	0.19-0.22	3-4	0.36-0.43	2	R, S

Table 1. Continued

Taxon	Origin and number of specimens	Length of lamina volsellaris (mm)	No. of setae on lamina volsellaris <sup>a</sup>	Digitus/lamina volsellaris length	No. of apical teeth of digitus	Shape of digitus <sup>b</sup>
<i>Microplitis manilae</i> Ashmead	Taiwan (2)	0.16	2-3	0.42-0.46	2	R, S
<i>Microplitis ratzeburgii</i> (Ruthe)	Japan (1)	0.27	5	0.39	2	R, C-S
<i>Microplitis sispes</i> Nixon	Canada (1)	0.30	3-4	0.33	2	R, S (Fig. 31)
<i>Snellenius theretrae</i> (Watanabe)	Japan (2)	0.30-0.32	4-5	0.41-0.45	2	R, S (Fig. 32)
<b>CARDIOCHILINAE</b>						
<i>Cardiochiles japonicus</i> Watanabe	Japan (2)	0.43-0.50	4-5	0.44-0.51	8	R, C-S (Fig. 51)
<i>Cardiochiles nigriceps</i> Viereck	USA (1)	0.39	3-4	0.52	10	R, S (Fig. 52)
<i>Cardiochiles szepligetii</i> Enderlein	Taiwan (2)	0.30	4-6	0.44-0.49	7	R, C-S
<i>Hartemita muirii</i> (Fullaway)	Japan (1)	0.29	7-8	0.48	5	R, S (Fig. 53)
<b>MIRACINAE</b>						
<i>Mirax captodisciae</i> Walley	Canada (1)	0.10	(5)	0.43	2	R, S (Fig. 54)
<i>Mirax insularis</i> Muesebeck	Dominica (1)	0.09	(4-5)	0.46	2	R, S
<i>Mirax mogrus</i> Papp	Japan (3)	0.12-0.16	(4-6)	0.40-0.44	2	R, S (Fig. 55)

<sup>a</sup> Number of alveoli without a seta is indicated in parentheses.

<sup>b</sup> Apex: A = acute and directed dorsally, O = somewhat obtuse and directed dorsally, N = narrowly truncated, not strongly directed dorsally, R = round or broadly truncated, T = tubiform and curved dorsally. Ventral edge: C = strongly convex, S = almost straight or slightly convex.

volsellaris with 1-7 (usually 2-4) setae (Table 1). Cuspid glabrous, separated from digitus. Relative length of digitus to lamina volsellaris 0.34 to 0.62 (Table 1). In *Choeras*, *Hypomicrogaster*, *Iconella*, *Paroplitis* and *Pseudapanteles*, digitus arched dorsally or crescent-shaped, distinctly convex ventrally, with a pointed apex directed dorsally or laterally (Figs. 14-17, 21, 23); in *Hygroplitis*, *Microgaster* and *Rhygoplitis*, digitus arched dorsally as in the preceding genera but the apex somewhat obtuse (Figs. 18-20, 25); in *Prasmodon* and *Xanthomicrogaster*, digitus not or only slightly convex ventrally, not crescent-shaped, but the apical portion obviously bent dorsally (Figs. 22, 28). In *Sathon*, digitus slightly convex ventrally, not crescent-shaped, with a round or narrowly truncated apex (Figs. 24, 27), or slender, tubiform and abruptly curved dorsally (Fig. 26). Apex of digitus with 2-4 teeth, but the number of the apical teeth up to 5 in *Prasmodon* (Table 1).

**Microgastrinae: Forniciini.** Lamina volsellaris with 2 setae (Table 1). Cuspid glabrous and separated from digitus. Relative

length of digitus to lamina volsellaris 0.46 to 0.53. Digitus weakly convex ventrally, not crescent-shaped, with a round apex bearing 3-4 teeth (Fig. 29).

**Microgastrinae: Cotesiini.** Lamina volsellaris with 1-15 setae or setal alveoli, usually with less than 8 setae except for *Cotesia*, in which it has 6-15 setae (Table 1, Fig. 56). Cuspid glabrous and separated from digitus, but the intermediate membranous area is narrow in *Deuterixys* (Fig. 38) and *Vananus* (Fig. 49). Relative length of digitus to lamina volsellaris 0.27 to 0.54 (Table 1). Digitus almost straight or weakly convex ventrally, not crescent-shaped, with a round apex (Figs. 34, 36-50), or with a narrowly truncated apex in *Lathrapanteles* (Fig. 35). Apex of digitus with 2-6 (usually 2-4) teeth (Table 1).

**Microgastrinae: Microplitini.** Lamina volsellaris with 2-5 setae (Table 1). Cuspid glabrous and separated from digitus. Relative length of digitus to lamina volsellaris 0.33 to 0.49 (Table 1). Digitus almost straight or weakly convex ventrally, not crescent-shaped, with a round apex bearing 2-3 teeth (Figs. 30-33).

**Cardiochilinae.** Lamina volsellaris with 3–8 setae (Table 1). Cuspis separated from digitus, and bearing a group of alveoli without seta (Fig. 52). Relative length of digitus to lamina volsellaris 0.44–0.52. Digitus round apically and not or weakly arched dorsally (Figs. 51–53), with 5–10 apical teeth.

**Miracinae.** Lamina volsellaris with 4–6 alveoli, invariably without seta. Cuspis glabrous, separated from digitus. Relative length of digitus to lamina volsellaris 0.40–0.46. Digitus broadly truncated apically, slightly arched dorsally, and invariably with 2 apical teeth (Figs. 54–55).

### Polarity of Character States

Based on the conditions observed in the outgroups, Cardiochilinae and Miracinae, the polarity of character states in the Microgastrinae is suggested as follows:

1. **Number of setae (or setal alveoli) on lamina volsellaris.** The plesiomorphic condition is perhaps 3–6. Loss and acquisition of setae are found both in the Microgastrini and Cotesiini. *Cotesia* is aberrant in always having numerous volsellar setae (Fig. 56), and also some other genera of the Cotesiini (*Glyptapanteles*, *Lathrapanteles*, *Protapanteles*) and *Sathon* (Microgastrini) often have 7 or more setae.
2. **Articulation of digitus with cuspis.** Separation of the digitus from the cuspis is apparently plesiomorphic. The fusion of these lobes is found only in the genus *Miropotes* (Apantelini).
3. **Relative length of digitus to lamina volsellaris.** Medium sized digitus, 0.4–0.5 of the lamina volsellaris in length, is probably plesiomorphic. A comparatively long digitus (0.55 or more times as long as the lamina volsellaris) was found in some genera of the Apantelini and Microgastrini.
4. **Shape of digitus.** The digitus, not distinctly arched dorsally, with a round or broadly truncated apex is probably ple-

siomorphic. The digitus found in the Apantelini and Microgastrini is apomorphic, being crescent-shaped with a sharp (occasionally slightly obtuse) apex directed dorsally or laterally.

5. **Number of apical teeth of digitus.** A plesiomorphic condition cannot be defined, because the teeth vary in number from 2 in the Miracinae to 5–10 in the Cardiochilinae.

### Reassessment of Mason's Tribal System

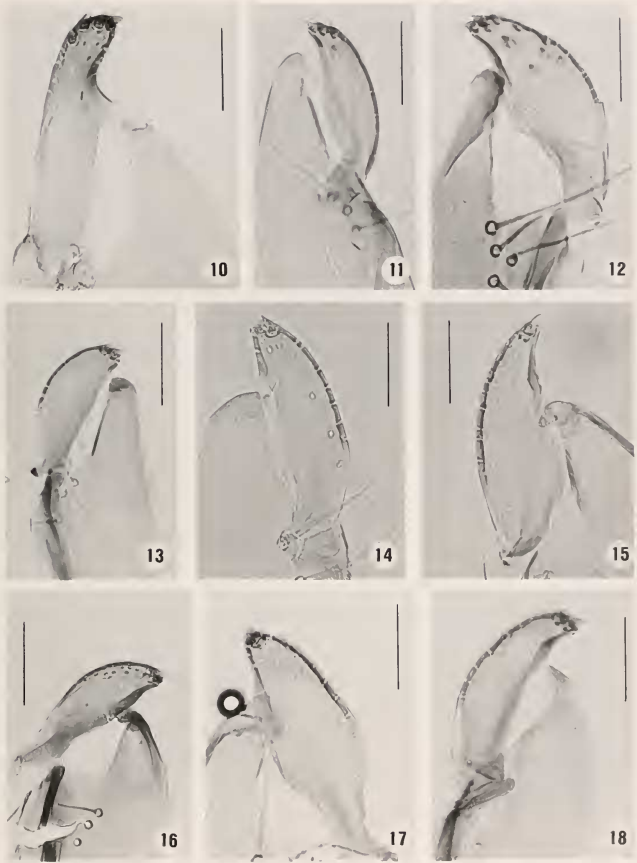
Although Mason (1981) postulated that his tribes Apantelini and Microgastrini form a monophyletic group, he did not suggest any credible synapomorphies for the assemblage (Walker et al. 1990). Austin (1990), however, pointed out that the ventromedially membranous, folded and often expandible hypopygium is probably a synapomorphy for a clade including most, definitely not all, of Mason's Apantelini + Microgastrini.

Moreover, the monophyly of Apantelini + Microgastrini is most likely to be supported by the crescent-shaped or arched digitus with its sharp (or slightly obtuse) apex being directed dorsally or laterally. In some aberrant genera (*Illidops*, *Miropotes*, *Pelicope* and *Xanthomicrogaster*), the digitus is not typically crescent-shaped, but the apical portion tends to be pointed dorsally or laterally.

Mason's tribe Apantelini has been distinguished from his Microgastrini by having no percurrent median carina on the propodeum. Most genera of the Apantelini doubtless form a monophyletic group supported by the anteriorly projecting lateral lobe of the metanotum (Mason 1981). However, some genera (*Miropotes*, *Sendaphne*, *Pelicope*, etc.) of the Apantelini are devoid of the apomorphy. At the same time, some genera (*Choeras*, *Clarkinella*, *Ico-nella*) of the Microgastrini show a similar if not homologous character state (Mason 1981). The percurrent median propodeal carina of the Microgastrini may be apomorphic, but the same condition is found

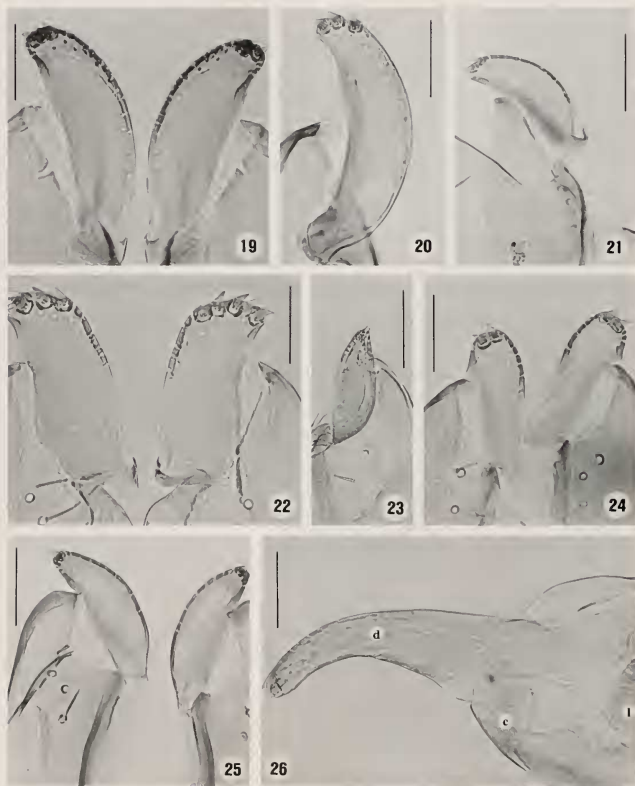


Figs. 1-9. Apical portion of volsella in the Apanteleini. 1, *Apanteles baldufi*. 2, *Apanteles cypris*. 3, *Austrocotesia delicata* (the whole of volsella). 4, *Dolichogenidea infima*. 5, *Dolichogenidea nixosiris*. 6, *Illidops* sp. 7, *Miopotes kilikulunis*. 8, *Miopotes thuraris*. 9, *Papanteles peckorum*. Abbreviations: c, cuspis; d, digitus; l, lamina volsellaris; r, volsellar ridge. Scale lines = 0.05mm.

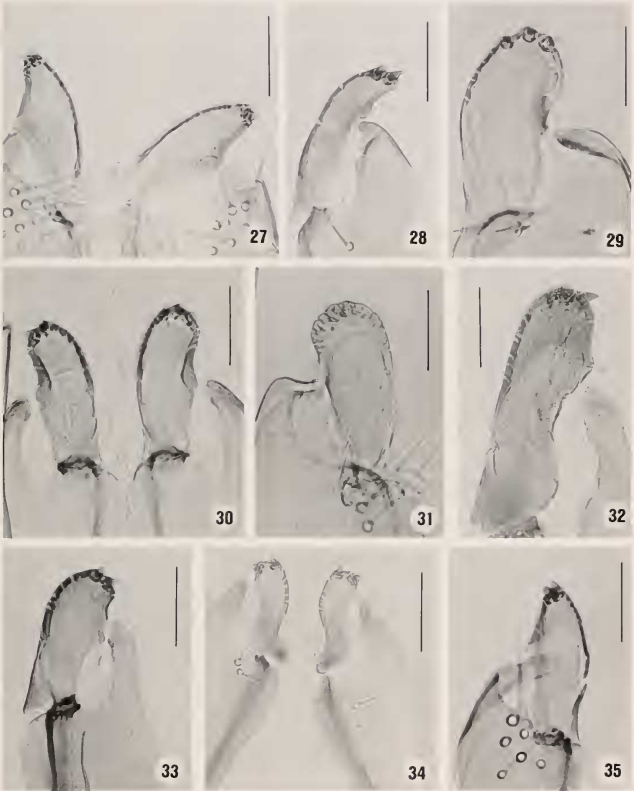


Figs. 10–18. Apical portion of volsella in the Apantelini (10–13) and Microgastrini (14–18). 10, *Pelicope yuc-camica*. 11, *Promicrogaster* sp. 12, *Sendaphne* sp. 13, *Pholetesor viminetorum*. 14, *Choeras psarae*. 15, *Choeras takeuchii*. 16, *Hypomicrogaster ecdytolophae*. 17, *Iconella etellae*. 18, *Microgaster australis*. Scale lines = 0.05mm.

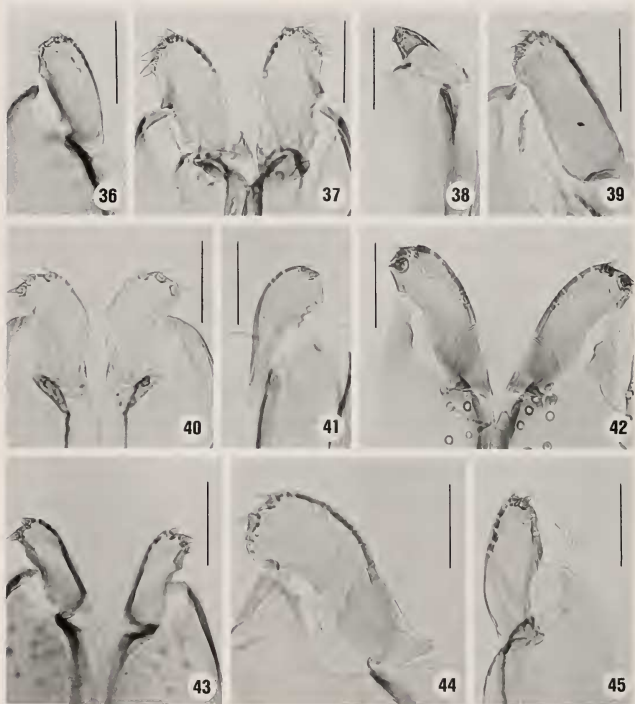




Figs. 19–26. Apical portion of volsella in the Microgastrini. 19, *Hygroplitis russatus*. 20, *Microgaster kuchingensis*. 21, *Paroplitis* cf. *wesmaeli*. 22, *Prasmodon* sp. 23, *Pseudapanteles annulicornis*. 24, *Sathon lateralis*. 25, *Rhygoplitis aciculatus*. 26, *Sathon neomexicanus*. Abbreviations: c, cuspis; d, digitus; l, lamina volsellaris. Scale lines = 0.05mm



Figs. 27–35. Apical portion of volsella in the Microgastrini (27–28), Forniciini (29), Microplitini (30–33) and Cotesiini (34–35). 27, *Sathon masoni*. 28, *Xanthomicrogaster* sp. 29, *Fornica ceylonica*. 30, *Microplitis atamiensis*. 31, *Microplitis sispes*. 32, *Snellenius theretrae*. 33, *Alloplitis completus*. 34, *Buluka achterbergi*. 35, *Lathrapanteles fuscus*. Scale lines = 0.05mm.

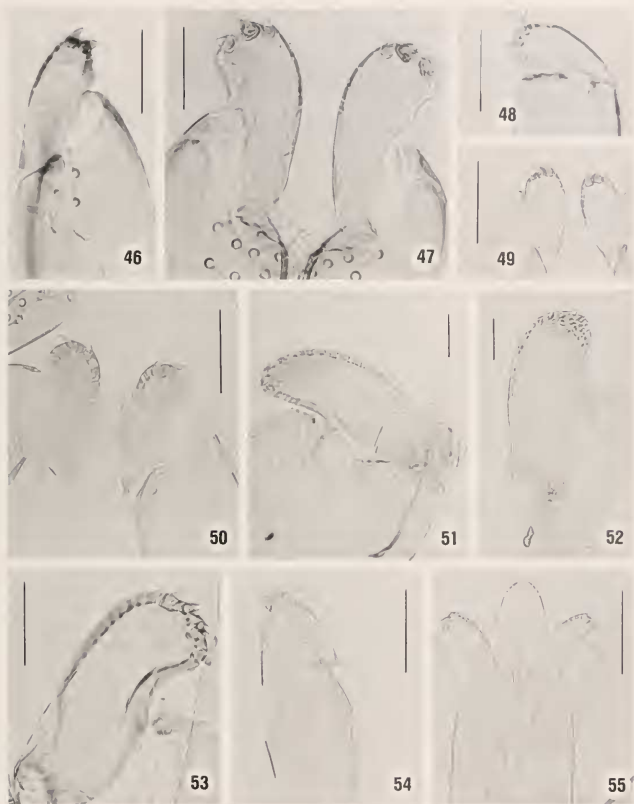


Figs. 36-45. Apical portion of volsella in the Cotesiini. 36, *Cotesia melanoscelus*. 37, *Cotesia tatehae*. 38, *Deuterrixys carbonaria*. 39, *Diolcogaster abdominalis*. 40, *Diolcogaster* cf. *spreti*. 41, *Distatrix papilionis*. 42, *Exix mexicana*. 43, *Protapanteles lymantriae*. 44, *Protomicropplitis medius*. 45, *Rasivalva rugosa*. Scale lines = 0.05mm.

in many other Microgastrinae as well as in the Cardiochilinae and Miracinae. Therefore, the sister-group relationship of the Apantelini and Microgastrini is unsupported.

Although the hypopygium of *Austrocotesia*, *Hygroplitis* and most *Pholeteor* is

evenly sclerotized (plesiomorphic), their digitus is apomorphic in shape. They may be basal lineages of the clade Apantelini + Microgastrini, or they may have secondarily lost the membranous median fold of the hypopygium. The placement of *Prasmodon* in this clade is uncertain, be-



Figs. 46–55. Apical portion of volsella in the Cotesiini (46–50) and in the Cardiochilinae (51–53) and Miracinae (54–55). 46, *Glyptapanteles aliphera*. 47, *Glyptapanteles liparidis*. 48, *Venanides xeste*. 49, *Venanus pinicola*. 50, *Wilkinsonellus striatus*. 51, *Cardiochiles japonicus*. 52, *Cardiochiles nigriceps*. 53, *Hartemita muirii*. 54, *Mirax captodisciae* (the whole of volsella). 55, *Mirax mogrus* (including aedeagus). Scale lines = 0.05mm.

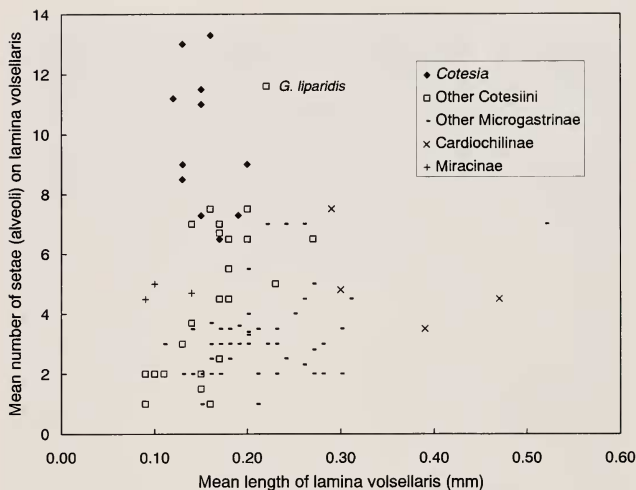


Fig. 56. Number of setae or setal alveoli on lamina volsellaris in the Microgastrinae and its outgroups, Cardiochilinae and Miracinae.

cause it lacks the membranous hypopygium and also its digitus is not evidently apomorphic.

Also, *Sathon* has been placed in the Microgastrini even though its hypopygium is evenly sclerotized (Mason 1981, Williams 1985, 1988). The digitus of *Sathon* varies in shape but is always different from the crescent-shaped digitus of most Apantelini and Microgastrini; it is round apically in *S. lateralis* like in many of the Forniciini + Cotesiini + Microplitini, narrowly truncated in *S. masoni* very similar to that of *Lathrapanteles fuscus* (Cotesiini), or aberrantly tubiform in *S. neomexicanus*. Hence, *Sathon* shares no definite synapomorphies with the rest of Apantelini + Microgastrini. On the other hand, the metanotum of *Sathon* shows a simple and glabrous anterior margin, along with a widely ex-

posed scutellar phragma (Williams 1988); such an apomorphic state is frequently found in the Cotesiini (e.g., *Glyptapanteles*, *Lathrapanteles*, *Protapanteles*) but not in the Apantelini nor Microgastrini (Mason 1981). Moreover, the larval papules of the larval skin lack long spines (apomorphic state) in *Sathon* as in most Cotesiini and Microplitini. These circumstantial pieces of evidence suggest that *Sathon* belongs to the Cotesiini instead of to the Microgastrini.

Mason's tribes of Forniciini, Cotesiini and Microplitini are commonly characterized by several apomorphies: ovipositor sheath (3rd valvula) attached to 2nd valvifer subbasally, 2nd valvifer widened apically, larval mandible with no teeth or with less than 15 (usually a few weak) teeth subapically, and papules of larval

skin without long spines (Short 1953, Mason 1981, Williams 1985, Walker et al. 1990). Mason (1981) indicated additional apomorphies (e.g., setae of ovipositor sheath restricted apically, ovipositor abruptly narrowed subapically) while these may be related to the reduction of the ovipositor in length. In fact, the genus *Lathrapanteles*, which has a long ovipositor, lacks some of the apomorphies (Williams 1985). Besides the morphological apomorphies, absence of the final ectophagous stage of larvae may be also autapomorphic for the Cotesiini and Microplitini, because the ectophagous phase is common in the Apantelini and Microgastrini as well as in the Cardiochilinae and Cheloniinae (Huddleston and Walker 1988, Shaw and Huddleston 1991).

Mason (1981) divided this clade into the Forniciini, Cotesiini and Microplitini, without indicating any reliable autapomorphies for the Cotesiini (Walker et al., 1990). In the Forniciini, Microplitini, and the *Diolcogaster* genus-group of the Cotesiini, the apical smooth band of the scutellum is almost always interrupted medially by a punctate or rugose area (Nixon, 1965, Mason 1981, Austin 1992); this condition is possibly apomorphic within the clade Forniciini + Cotesiini + Microplitini because, as in the remainder of this clade, the apical smooth band of the scutellum is continuous in the Apantelini and Microgastrini (except for *Illidops*). Moreover, females of *Fornicia* (Forniciini), *Alloplitis* (Microplitini) and at least two genera, *Diolcogaster* and *Exix*, of the *Diolcogaster* genus-group (Cotesiini) share apomorphic, ventral sensory fields on the middle and subapical flagellomeres in common (Mason 1981). Therefore, it is most likely that the Cotesiini is paraphyletic when the Forniciini and Microplitini are not included.

In conclusion, Mason's framework of two main clades (Apantelini + Microgastrini, and Forniciini + Cotesiini + Microplitini) in the Microgastrinae is essentially

supported while monophyly of each tribe is not sustained.

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